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Spatial positioning in the selfish herd

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Abstract

The anti-predator benefits of grouping are relatively well understood; however, predation risk often differs for individuals that occupy different positions within a group. The selfish herd hypothesis describes how individuals can reduce risk of predation by moving to specific positions within the group. In existing theory, this movement occurs through the adoption of possible 'movement rules' that differ in their cognitive complexity. Here, we investigate the effectiveness of different previously-suggested rules in reducing risk for central and peripheral individuals within a group. We demonstrate that initial spatial position is important in determining the success of different risk-reducing movement rules, as initially centrally positioned individuals are likely to be more successful than peripheral ones at reducing their risk relative to other group members, regardless of the movement rules used. Simpler strategies are effective in low density populations; but at high density, more complex rules are more effective. We also find that complex rules that consider the position of multiple neighbors are the only rules that successfully allow individuals to move from peripheral to central positions, or maintain central positions, thus avoiding predators that attack from outside the group. Our results suggest that the attack strategy of a predator should be critically important in determining prey escape strategies in a selfish herd context; and that prey should modify their behavioral responses to impending attack in response to their position within a group.

Keywords: anti-predator behavior, aggregation, grouping, periphery, group centre, predation risk, individual-based model.

Introduction

Predation risk has been widely demonstrated to be a key factor driving the behavioral ecology of many animals (Caro 2005). One of the most-studied responses to heightened predation risk is grouping behaviors (Krause and Ruxton 2002). It is widely recognized that under heightened predation risk groups tend to be larger (Hager and Helfman 1991; Hoare et al 2004), more compact (Foster and Treherne 1981; Spieler and Linsenmair 1999; Watt et al. 1997), and individuals within groups tend to be more closely assorted by phenotype (Allan and Pitcher 1986; Theodorakis 1989; Szulkin et al. 2006; Croft et al. 2009). The selfish herd theory (Hamilton 1971) has been particularly influential in understanding such facultative aggregation in response to heightened predation risk.

The selfish herd hypothesis assumes that the relative predation risk of two individuals can be determined by comparison of the areas around each that is closer to the focal individual than to any other individuals: the *domain of danger* (DOD). Predatory attacks are assumed to be launched from random points within the environment, with all positions being equally likely to be launch points. If an attack is launched from within a particular individual's domain of danger, then that individual is assumed to be attacked and killed (Hamilton 1971). Thus, an individual prey's risk of predation is proportional to the size of their DOD; and to reduce predation risk, each animal should endeavor to reduce its DOD size relative to those of other individuals. This naturally leads to greater aggregation. More recent theoretical developments have focused on evaluating candidate behavioral 'movement rules' that cause individuals to reduce their DOD (Morton et al. 1994; Viscido et al. 2002; James et al. 2004; Wood and Ackland 2007; Morrell and James 2008).

The costs and benefits of grouping are not always experienced equally by all members of a group (Krause and Ruxton 2002). The theory of marginal predation (Hamilton 1971; Vine 1971) suggests that if predators attack the closest prey, then those on the edge of groups should experience greater risk, either because they have the largest DODs, or because predators are simply more likely to attack from outside a group than within it. Simulation models have shown that peripheral individuals should be at greater risk (Bumann et al. 1997; Morrell and Romey 2008), and empirical evidence suggests that this is indeed often but not always the case (Okamura 1986; Rayor and Uetz 1990; Šálek and Šmilauer 2002; Stankowich 2003; Romey et al. 2008, but see Parrish 1989; Quinn and Cresswell 2006). An individual's position within a group, therefore, might often be expected to affect its response to a predation event. Previous theory has assumed that all individuals follow the same movement rules in response to cues of an imminent predatory attack. Here, we investigate how position within a group affects anti-predator behavior in the context of the selfish herd, by investigating the success of a 'mutant' movement rule invading a group of individuals using a different movement rule in response to a predation threat (see methods for descriptions of different movement rules). We will consider both situations where predation occurs from a position outside the group, as well as situations where attacks can be launched from any point in space. We consider how the position (central or peripheral) in which an individual finds itself when it initially responds to the predation threat affects the success of different movement rules in reducing relative DOD areas. We predict that starting position will influence the relative success of different movement rules in reducing DOD areas and therefore predation risk of individuals.

Previous theoretical developments exploring the effectiveness of different movement rules evaluated the effectiveness of such rules purely in terms of their ability to reduce the mover's DOD. This is reasonable since, as originally formulated, the Selfish Herd theory assumed that predatory attacks were equally as likely to be launched from any position within the environment. Many subsequent works have retained this assumption (e.g. Morton et al. 1994; Viscido et al. 2002; James et al. 2004; Morrell and James 2008), and we use this approach here to allow for comparison with previous studies. In some circumstances (for example, avian predators attacking prey from above; e.g. Quinn & Cresswell 2006), such an approach is appropriate. However, as James et al. (2004) argue, in many predator-prey associations attacks are generally unlikely to occur from positions within the group. For example, as a group moves through its environment, it is likely that an ambushing predator waiting in the path of the group would be detected before the group moves over its position. Hence, in many ecological situations predatory attacks on grouped prey will occur exclusively from outside the group. In such circumstances, there is a strong premium to a group member in being in the interior of the group, since peripheral individuals will be at much greater risk. Accordingly, in a second analysis, we investigate how effective different movement rules are at placing their user within the centre of a group.

Methods

Model framework

We use the modeling framework described by James et al. (2004) and Morrell & James (2008) as the basis for our simulation model of aggregation behavior, and provide a

summary here. N point-like agents (the prey) are placed in a two-dimensional circular arena of radius R following a random uniform distribution. That is, initially, there is no aggregation, and individuals are placed without consideration to the positions of others. Population density, d, is described by $N/\pi R^2$. In each simulation, N_m agents are allocated a 'mutant' movement rule, while N_p agents are allocated a 'population' movement rule ($N_m + N_p = N$). We use the 'limited DOD' (LDOD) framework to describe relative predation risks, this is thought to more realistically portray individual predation risk than the traditional definition, in which some individuals have infinite DODs (James et al. 2004; Morrell and James 2008). The conventional, or *unlimited DOD* (UDOD) of an agent in 2D space is defined as the region closer to that agent than any other, and is the measure of individual predation risk introduced in Hamilton (1971). The *limited* DOD (LDOD) of an agent is the region that is inside both the UDOD and inside a circle of radius r centered on the agent (see figure 1 for illustration of UDODs and LDODs). For each agent, we calculate the area (A) of their LDOD. The maximum LDOD area, which occurs only when the agent is at least $2r$ from any others, is given by $A_{max} = \pi r^2$. LDOD areas are reduced by any bisector generated by an individual within a distance of $2r$. We also calculate UDOD areas using Voronoi tessellations: this information is later used to identify central and peripheral agents.

Movement rules

We consider a subset of previous-proposed movement rules, encompassing variation in complexity: Nearest Neighbor (NN; Hamilton 1971), multiple nearest neighbors (3NN; Morton et al. 1994) and local crowded horizon (LCH; Viscido et al. 2002). Under the NN rule, agents move directly towards their closest neighbor, under the 3NN rule, individuals move towards the average location of their three closest neighbors, and under the LCH rule, the

position of multiple neighbors is taken into account, with closer ones having the greatest influence on movement direction. To describe this effect we weight the influence of individuals using the perception function suggested by Viscido and coworkers (2002) as being the most biologically plausible: $f(x) = \frac{1}{1+0.375x}$, where *x* is the distance from the focal individual. An individual's movement direction is determined solely by its movement rule: agents do not receive any directional information on predator attack direction, and the habitat contains no refuge areas. That is, at the start of a simulation (*t* = 0) the prey are assumed to initiate their behavioral rules in response to picking up cues of an imminent predatory attack. These cues inform the prey that an attack is likely in the immediate future, but they do not provide information as to the position from which the attack will be launched. All prey are assumed to pick up these cues at the same time. The warning cues might be the fleeing or alarm calling of nearby heterospecifics, for example. We then simulate the movement of the animals from this point until the attack actually occurs. Simulations end at the point of attack ($t = t_{max}$), where the relative vulnerabilities of individuals are evaluated.

In each timestep *t*, until a maximum t_{max}, each agent identifies its target location, based on the movement rule it is following, and then moves towards it at a speed of 0.15m/s (James et al. 2004; Morrell and James 2008). Each agent updates its target location and direction in every timestep, and a timestep in our simulations lasts 0.1 seconds. After every timestep and for every individual we calculated both the LDOD area and the UDOD area. UDOD areas are used to define central and peripheral positions (peripheral individuals have infinite UDODs), and LDOD areas measure individual predation risk. Figure 1 (a and b) illustrates a

group of animals with UDODs (a) and LDODs (b) marked. We ran 1000 simulations for each possible pairwise combination of mutant versus population movement rules (6 combinations in total). However, we standardized starting positions between movement rules, such that all mutant versus population combinations were run with the same set of 1000 initial positions. All simulations were programmed in C. Resulting data was analysed using Matlab® R2007b (Mathworks 2007).

Our model clearly does not accurately depict any one particular real-world system. Our aim was to explore the principles which may underlie the 'movement towards conspecifics' aspect of anti-predator responses (seen in the real world in the aggregation of prey animals under threat of predation; see the introduction for empirical examples of this). As one of our aims was to provide comparison with, and development of, previous selfish herd models, we explore the principles in the same modelling framework as used by previous works. Although, for simplicity, we explore a two-dimensional landscape in our model, our results could certainly be extrapolated from to 3D ones (such as fish shoals or bird flocks).

Research questions

We use the data from the model to answer two questions: 1) how does starting position (peripheral or central) influence the success of a mutant invading a population in terms of its predation risk relative to other group members (proportion of total LDOD area occupied by the mutant and an average member of the population), thereby avoiding predators that attack randomly; and 2) how successful are the different movement rules in allowing an individual to move from peripheral to central positions, thereby avoiding predators which attack from outside the group? The first of these complementary questions follows the

traditional approach of comparing DOD areas between individuals, while the second explores risk avoidance when predators are expected to attack from outside the group.

Approach 1: Avoiding risk by reducing LDOD area relative to others: the effect of spatial position

To assess relative predation risk and the ability of a mutant strategy to invade a population strategy, at each timestep we first calculated the total LDOD area, A_{tot} (the sum of A for all individuals). We then calculated the proportion of A_{tot} occupied by the mutant, and the proportion occupied by each population member. We then calculated the mean value for the population. Finally, we calculated the difference between the proportion of A_{tot} occupied by the mutant, and the mean proportion occupied by an average population member. This was repeated for each timestep in each replicate simulation. A positive value indicates that the mutant occupies a larger proportion of the total area than an average population member, and a smaller value indicated that the mutant occupies a smaller area and can successfully invade the population. This approach assumes that predation risk is based only on LDOD area (i.e. that predators can attack anywhere within the group, and follows the same approach used in previous studies of the selfish herd (Hamilton 1971; Morton et al. 1994; Viscido et al. 2002; James et al. 2004; Morrell and James 2008). Previous work has shown that both population size (N) and density (d) can affect rule success (Morrell & James 2008) and we vary these here, predicting that complex rules will perform better in smaller, higher density populations.

We are interested in how spatial position affects change in LDOD area (and therefore reduction in relative risk). We define a peripheral individual as any member of a group with

an infinite domain of danger, using the UDOD framework. Any individual with a finite domain of danger is considered central (this is equivalent to using the minimum convex polygon approach to defining peripheral individuals within a group; Krause and Ruxton 2002; Krause and Tegeder 1994). We record the starting position (peripheral or central) for the mutant individual in each simulation, and use this information to split the data collected on LDOD areas. We then calculate the mean and standard error across replicates for mutants that were peripheral (414/1000 replicates when N=20, 233/1000 replicates when N=50), and central (586 and 767 replicates respectively) at the start of the simulation. We also calculate the mean and standard error across all individuals, regardless of whether they started in a peripheral or central position. For visual simplicity, we subsample our results and show only the differences in LDOD areas at 2 points in time, following Morrell & James (2008): after 2 seconds of movement (t_{max}=2, figure 2, left hand column) and after 10 seconds of movement (t_{max}=10, figure2, right hand column). The first of these represents a "early attacking" predator that can complete an attack within 2 seconds of cues of its presence being detected; the second representing a "later attacking" predator that requires longer. Biologically this variation might be interpreted as reflecting how quickly an ambushing predator can close the distance from the point that it breaks cover to the point where it can complete an attack: an early-attacking predator can cover this distance quickly, so aggregating prey have relatively little time to respond to any cues of imminent attack (which are triggered when the predator breaks cover).

Approach 2: Avoiding risk by moving to the group centre

For a movement rule to be considered successful in terms of reducing the risk of peripheral predation for individuals using that rule, the proportion of mutant individuals occupying

peripheral positions should be lower than expected by chance once movement has begun (see below). Using the definition of peripheral above, for each individual (mutant and population member) within each group, we record whether their position is peripheral or central at the start of the simulation, after 2 seconds of movement, and after 10 seconds of movement.

For each replicate simulation, we calculate the proportion of individuals occupying central positions, and the proportion occupying peripheral ones. We also calculate the proportion of the 1000 simulations where the mutant individual occupies a central position and the proportion where it occupies a peripheral one. This allows us to assess whether mutants are more or less likely to occupy central positions than would be expected by chance. If the probability of a mutant occupying a peripheral position is lower than the mean proportion of the group that is on the periphery, then the mutant is more likely to occupy a central position than would be expected by chance. For example, if on average, 40% of the group members are positioned on the periphery at any given point in the movement sequence, we would expect a single mutant within that group to be on the periphery in 40% of the simulations. If the mutant is peripheral in less than 40% of the simulations, this is lower than one would expect by chance, and the rule is successful at moving the individual to the centre of the group. If it is peripheral in more than 40% of the simulations, then the rule is unsuccessful. Figure 1 (c and d) illustrates the positions of the individuals in a group of animals before (c) and after (d) movement, demonstrating how a peripheral mutant can move to a central position.

Results

Approach 1: Avoiding risk by reducing LDOD area relative to others: the effect of spatial position

We define a successful invasion as one where the difference in the proportion of the total LDOD area between the mutant and the population (see methods) is negative. In figure 2, equal success occurs at 0, indicated by a horizontal dashed line. If the data point representing the mean difference lies below this line (i.e. is negative), the mutant can invade. If the point is above this line (i.e. is positive), the population is stable against invasion.

Firstly we consider the success of mutant individuals in obtaining smaller LDODs than population members, regardless of their starting position (filled circles in figure 2), and find that there are clear differences in the ability of mutants to successfully invade a population. For example, in a small, low density population (N=20, d=2), and if predators attack after 2 seconds of movement (figure 2a), the only mutants able to invade are NN mutants in LCH populations, and 3NN mutants in LCH populations. In all other mutant-population combinations the population is stable against invasion. In contrast, after 10 seconds of movement (figure 2b) NN populations are unstable and can be invaded by mutants using both 3NN and LCH.

However, if we divide the data and consider separately those mutants that start in the centre of the group (open circles), and those that start on the periphery (open diamonds), somewhat different patterns emerge. In general, centrally positioned mutants are more capable of invading populations than are their peripherally positioned counterparts. That is (regardless of behavioural rules adopted by individuals) those individuals that – for

whatever reason – find themselves away from the periphery when movements begin are at an advantage. Indeed, if a mutant is on the edge of the group at the start of simulations, it is unable to invade the group after 2 seconds of movement (i.e. if predators attack early; figure 2a, open diamonds). If predators attack late (after 10 seconds of movement, figure 2b), then NN populations become unstable against even peripheral mutants using 3NN and LCH, and are themselves unable to invade populations using these strategies, regardless of their starting position.

We also considered the impact of altering the starting density and size of the population on the relative invasion success of peripheral and central mutants (figure 2). After 2 seconds of movement (figure 2, left hand column), increasing the starting density of the group (figure 2a, c and e) results is a decrease in performance for NN mutants; they become increasingly less able to invade populations using other strategies, and increasingly susceptible to invasion by 3NN and LCH mutants. Centrally positioned mutants continue to be more successful in their invasion than peripheral ones; in particular, central mutants using simpler rules are able to invade a population using more complex rules. If predators attack later (after 10 seconds, figure 2, right hand column), then increasing population density results in increased stability of complex rules, and increased invasion success of complex rules (figure 2b, d and f). Even peripheral mutants using more complex rules are able to invade populations using simpler rules.

Increasing population size has similar effects to decreasing population density (figures 2g and h). Increasing group size from 20 to 50 individuals (while controlling for density; comparing figures 2c and 2g) suggests that in larger populations, simpler rules are more

easily able to invade. For example, considering all mutants, NN can invade LCH after 2 seconds of movement in a group of 50 (figure 2g) but not in a group of 20 (figure 2c). After 10 seconds of movement (figure 2, right hand side) we see decreased stability of populations using complex rules as population size increases (figure 2d and h). For example, centrally positioned 3NN mutants can invade LCH populations at N=50 (figure 2h) but not at N=20 (figure 2d), and 3NN populations are stable against invasion by central LCH mutants at N=50, but not at N=20.

Approach 2: Avoiding risk by moving to the group centre

When we consider the relative proportions of mutants and population members occupying peripheral positions, we find that for all population densities studied, the results are similar (figure 3). NN mutants are more likely to occupy peripheral positions after 2 and 10 seconds of movement than expected by chance, when attempting to invade both 3NN and LCH populations. Conversely, both 3NN and LCH mutants are less likely to occupy peripheral positions in primarily NN groups (figure 3). LCH is also less likely to occupy peripheral positions in NN3 groups, while NN3 mutants are more likely to occupy peripheral positions in LCH groups. These patterns hold when the group is sampled at 2 or 10 seconds, and are more pronounced as the starting density of the group increases (figures 3b and c), suggesting that LCH is the most successful method of occupying central positions, followed by 3NN. There is also very little effect of increasing population size (to N=50): patterns remain the same, although overall proportions of peripheral individuals are reduced in comparison to smaller groups as would be expected (not shown).

Discussion

Our results suggest that the position of an individual within a group is critically important in determining the success of movement rules in allowing the individual to avoid predation. If we consider predation risk in terms of relative LDOD area (approach 1), and assume that predators attack from a randomly-chosen position (including positions within the group, with a probability dependent on LDOD area; Hamilton 1971), then we see patterns where the density of the group strongly affects the success of different movement rules. In low density populations, simple strategies are able to invade populations using more complex strategies, and are stable against invasion when predators attack rapidly, but more complex strategies succeed when predators attack more slowly. In a previous paper, similar patterns were demonstrated, whereby individuals using simple strategies could benefit via the encounter-dilution effect (Turner and Pitcher 1986) in low density populations when predators attacked rapidly (Morrell and James 2008). In the encounter-dilution effect, all individuals in a group benefit equally from aggregation reducing the rate at which predatory attacks are launched. Here, we show a further benefit through selfish herd effects, where for each attack launched at a group an individual following a different movement strategy from other group mates can reduce its risk of being targeted (with the risk to others increasing).

However, if predators attack only from outside a group (approach 2), primarily targeting peripheral individuals, we find that the results differ. Simple rules (NN) no longer perform well against more complex rules as they do not allow individuals using them to gain central positions, and are more likely to mean that an individual that begins in the centre cannot maintain that position. Population density is no longer important in determining success

measured in this way. The more complex strategies perform significantly better in allowing individuals to gain and maintain central positions.

It is perhaps unsurprising that the more complex rules result in a higher proportion of individuals ending up in central positions. If we imagine a simple group of 3 individuals, an individual that chooses to move to the average location of its 2 companions will be aiming to end up between them (i.e. in the centre, although in a group of 3 in a 2-D environment, all will have infinite UDODs). Extending to larger groups and rules taking into account more neighbors, it becomes clear that complex rules will usually lead to movement towards the centre of the group. This will result in the kind of compaction of groups normally seen in the wild (Foster and Treherne 1981; Krause and Tegeder 1994; Watt et al. 1997; Spieler and Linsenmair 1999). If groups are primarily attacked from outside the group (Vine 1971), rather than from anywhere within the environment (Hamilton 1971), then one can imagine that movement towards the group centre will evolve, either as a rule in itself, or via a rule that involves a number of nearest neighbors (perhaps cognitively simpler than movement towards the centre, which would require knowledge of the positions of all individuals within the group rather than a few closest neighbors).

There may be some limitations, however, to the success of complex rules. Firstly, complex movement rules have been criticized on the grounds that they may be too difficult for animals to follow (Morton et al. 1994; Viscido et al. 2002; Morrell and James 2008), for example, individuals may be limited in their knowledge of the positions of other group members. Secondly, if animals are unaware of where a predator attack is likely to come from (i.e. if predators attack randomly and this sometimes represents an attack from

outside, and at other times an attack from within the area occupied by the group), then there may be a trade-off between moving towards central locations and reducing risk through, for example, encounter-dilution effects. Recent work studying sticklebacks attacking swarms of *Daphnia* has shown that denser areas of groups are more conspicuous to predators (Ioannou et al. 2009), yet individuals benefit from being in denser parts of groups through a perceptual inability of predators to target individuals within the group (the confusion effect; Krakauer 1995). Widely-spaced redshanks (*Tringa tetanus*) are also more likely to fall victim to sparrowhawk (*Accipiter nisus*) predators (Quinn and Cresswell 2006).

In some species, the ability of an individual to occupy central positions may be limited by dominance hierarchies within a group, as dominant individuals may force subordinate ones to the periphery (Hall and Fedigan 1997; Ruckstuhl and Neuhaus 2005; Hirsch 2007) where predation risk is higher. Thus, optimal movement strategies may differ between dominant and subordinate individuals: dominant individuals preferring a strategy that ensures they maintain central positions, subordinate ones preferring one that allows them to reduce their individual risk rapidly. The interaction between dominance and predation avoidance is an interesting route for further enquiry.

In other animal groups, an individual's position is not limited by dominance hierarchies, but may depend instead on factors such as hunger levels (foraging needs) and anti-predator defenses (Krause 1994; Romey 1995; Morrell and Romey 2008). Although central individuals are often safer from predation; they are also often subject to reduced feeding rates (Krause 1994). Predator attacks may therefore arise when a particular individual is in the group centre on some occasions, and the group periphery on others. Individual behavioral

responses to predators may therefore be flexible, allowing individuals to respond optimally depending on some measure of state. This suggests that the best movement strategy depends not only on position within a group, but also on the behavioral decisions of others. A well-protected central individual with a small domain of danger would benefit the most by maintaining that position: individuals moving towards it from the periphery would serve to reduce its domain of danger further through the compaction of the group, potentially reducing its relative risk, but the individual may also need to ensure that it is not pushed to the periphery of the group. A game-theoretical approach investigating the positions of individuals within groups before and after a predator attack may be useful here, and it is likely that anti-predator movement within real animal groups is much more complex than the movement rules so far proposed.

Our results demonstrate the importance of considering *how* a predation event may occur when considering the success of different anti-predatory aggregative behaviors. If predators preferentially target peripheral prey, then movement that takes an individual to a central position should evolve. If predators target based on other criteria, such as spacing, preferentially targeting more isolated prey, then a variety of escape rules may arise. The roles of dominance, state (hunger levels or anti-predator defenses) and the way they interact with predator avoidance have yet to be studied in the context of the selfish herd, and experimental work investigating the rules used by real animals is almost completely lacking (but see Krause and Tegeder 1994). However, the predictions provided by our theory should provide further stimulus to such empirical investigation.

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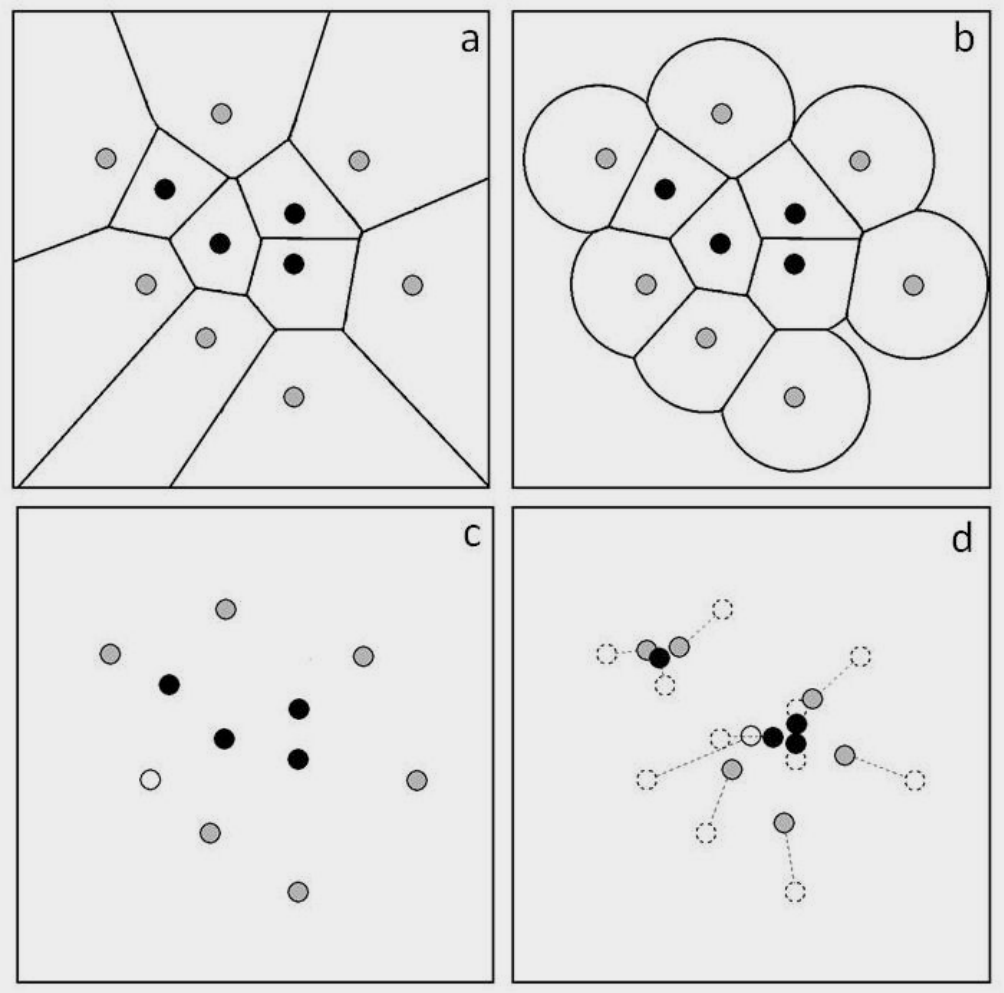
Figure legends

Figure 1: Approximate UDODs (a) and LDODs (b) for an illustrative group of 11 animals. Individuals with infinite UDODs and peripheral positions are colored grey, while those with finite UDODs and central positions are colored black. (c) and (d) illustrate the position of a mutant individual using LCH in a group of individuals using NN, showing how a mutant individual which begins on the periphery of the group (c) can acquire a central position after several seconds of movement (d). Initial positions are as in (a) and (b). Individuals starting in peripheral positions are grey, central individuals are black. Dotted lines in (d) do not show movement trajectories (which are usually curved), but simply link final positions to original start positions (open dashed circles). Individual colors in (d) represent starting position (central/peripheral/mutant). These figures are for illustrative purposes only and do not represent positions used in the analysis.

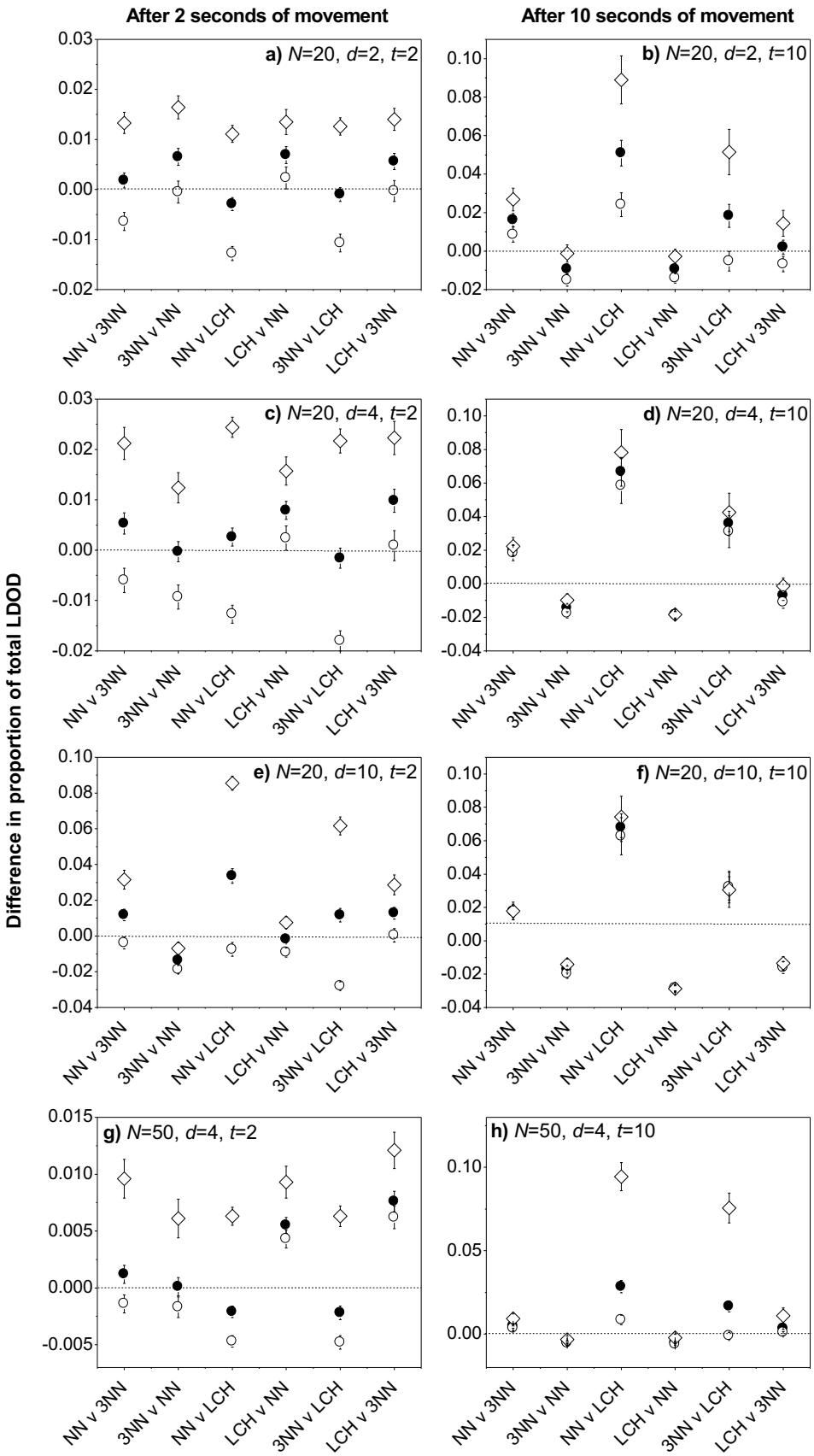
Figure 2: Mean (± 2 SE) difference between the proportion of total LDOD area occupied by the mutant and the mean proportion of total LDOD area occupied by population members, after 2 seconds (left hand column) and 10 seconds (right hand column) of movement. Data are presented as the mean for mutants starting in all positions (filled circles), plus those starting in central (open circles) and peripheral (open diamonds) positions. Panels show a single mutant (N_m = 1) in a group of 20 individuals (N = 20), at 3 population densities: **a & b**) d = 2; **c & d**) d = 4; **e & f**) d = 10, and **g & h)** a single mutant (N_m = 1) in a group of 50 individuals (N = 50) at d = 4. Where error bars are not shown, they are smaller than the size of the symbol.

Figure 3: Mean (± SD) proportion of a group of individuals occupying a peripheral position (open circles) and proportion of simulation runs where the mutant occupied a peripheral position (filled circles) at the start of the simulations, after 2 seconds and after 10 seconds, for each mutant-population combination. **a**) d = 2, **b**) d =4 **c**) d =10. Other parameter values: N=20, N_m = 1.

Figure 1

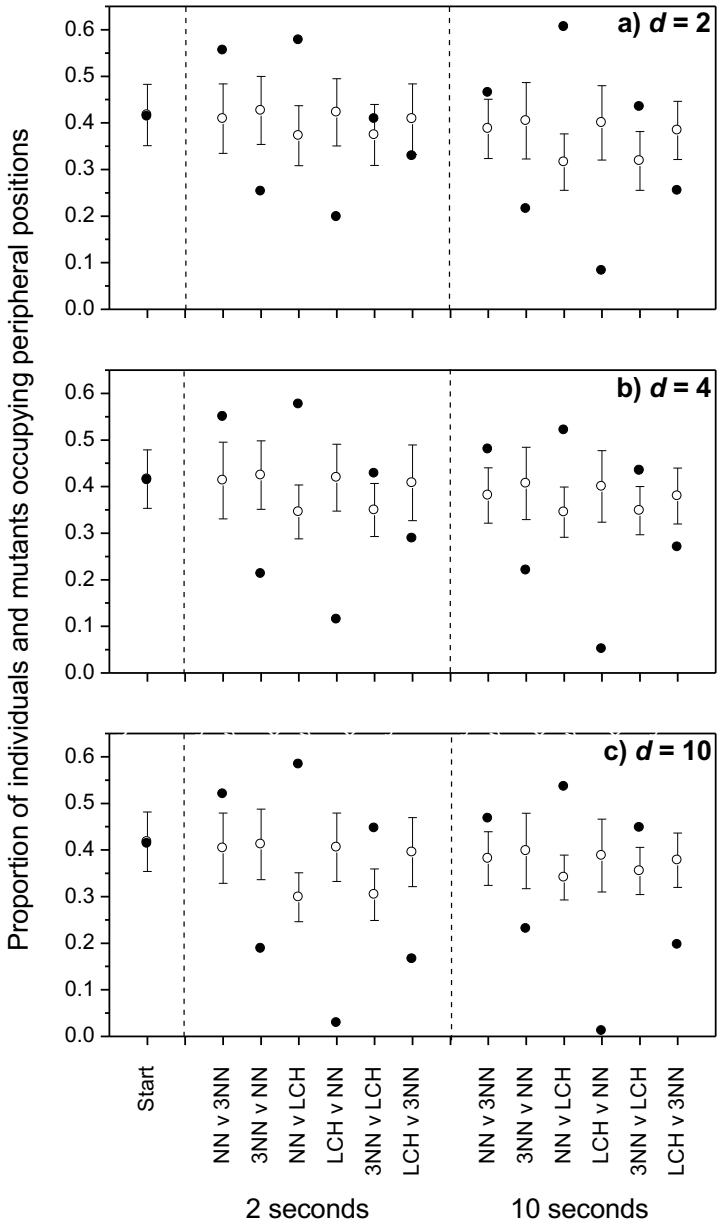


1 **Figure 2**


After 2 seconds of movement
After 10 seconds of movement
a) N=20, d=2, t=2
b) N=20, d=2, t=10
c) N=20, d=4, t=2
d) N=20, d=4, t=10
e) N=20, d=10, t=2
f) N=20, d=10, t=10
g) N=50, d=4, t=2
h) N=50, d=4, t=10
Difference in proportion of total LDOD
NN v 3NN
3NN v NN
NN v LCH
LCH v NN
3NN v LCH
LCH v 3NN
Movement rule: mutant v population

2

Figure 3


a) d = 2
b) d = 4
c) d = 10
Proportion of individuals and mutants occupying peripheral positions
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Start
NN v 3NN
3NN v NN
NN v LCH
LCH v NN
3NN v LCH
LCH v 3NN
2 seconds
10 seconds